

Topography may help explain faunal nestedness: a case study using Great Basin butterfly assemblages

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INTRODUCTION

Species that inhabit “islands” of terrestrial or aquatic habitat frequently have nested distributions (Wright et al. 1998). A nested biota is one in which the species present in depauperate locations are subsets of the species present in locations that are richer in species (Patterson & Atmar 1986). Early studies of nestedness documented that this distributional pattern is common across taxonomic groups and ecosystems (e.g., Patterson & Atmar 1986; Patterson 1987, 1990). Subsequent work has focused on refining metrics used to quantify nestedness and exploring factors that may produce nested distributional patterns (e.g., Cutler 1991; Wright & Reeves 1992; Atmar & Patterson 1993; Cook 1995; Cook & Quinn 1995; Lomolino 1996; Worthen & Rohde 1996; Brualdi & Sanderson 1999; Mac Nally & Lake 1999).

We dispute previous assertions that nested-subsets analyses hold little potential as practical conservation tools (Doak & Mills 1994; Boecklen 1997). The latter conclusions largely were drawn from studies that examined connections between species-area relationships and nestedness. If area is positively correlated with species richness and a biota is perfectly nested, then species richness should be greater in an extensive, contiguous site than in a collection of smaller sites. In principle, testing whether species richness of a nested assemblage increases with area indicates whether a single large or several small reserves would contain a greater number of species. In reality, biotas rarely are perfectly nested. The species richness of a nested system may or may not be significantly correlated with area, and environmental variables in addition to area may be significantly associated with species richness (Brown 1988; Doak & Mills 1994; Kadmon 1995; Rosenzweig 1995; Ricklefs & Lovette 1999). Therefore, nestedness analyses often cannot identify critical area thresholds (Boecklen 1997) or reliably predict the order in which species will be lost through ecological degradation (Doak & Mills 1994).

Evaluating the conservation potential of nestedness analysis solely with respect to reserve design, however, is unnecessarily limiting. For many years, conservation biologists have

considered the “single large or several small” (SLOSS) controversy relatively unproductive (Murphy 1989), although not entirely defunct (Honnay et al. 1999). Moreover, numerous features make nestedness analyses useful for land-use and conservation planning. First, regardless of whether one can identify species with the greatest sensitivity to habitat loss, the order of species disappearances in a nested community is at least partially predictable (Patterson & Atmar 1986). Second, it may be possible to identify certain species whose occurrence correlates strongly with the presence of other species. Third, some nestedness analyses can be used to identify “idiosyncratic” species with distributions that may be affected by environmental factors different from those affecting the assemblage as a whole (Atmar & Patterson 1993). Fourth, and perhaps most importantly, nestedness analyses can suggest, albeit via correlation, whether a given mechanism or environmental variable is likely to affect distributional patterns (e.g., Cook & Quinn 1995; Kadmon 1995). Differential nestedness among groups of species that vary in sensitivity to some human land uses, for example, may indicate that the activity in question is responsible for extirpations (Hecnar & M'Closkey 1997; Fleishman & Murphy 1999; Jonsson & Jonsell 1999). It may not always be possible to establish a cause-and-effect relationship between human activities and local species extinctions, but strong correlations can, at minimum, help refine hypotheses that can be tested with further manipulative experiments or observations.

Nestedness analyses are potentially promising as management and conservation tools because they provide information on patterns and suggest processes affecting not only species richness but also species composition. These data can be integral to decisions about how to maintain or maximize species diversity across a multiple-use landscape: which locations preferentially should be protected from human land uses, where more intensive human activities should be concentrated, and where investing in restoration or species reintroduction efforts may yield the greatest ecological returns (Freitag et al. 1997; Heikkinen 1998; Tardif & DesGranges 1998; Ricketts et al. 1999; Margules & Pressey 2000).

Of the diverse processes believed to generate nested distributions, nonrandom extinction and differential colonization historically have received the most attention (Patterson & Atmar 1986; Rabinowitz et al. 1986; Patterson 1990; Atmar & Patterson 1993; Cook & Quinn 1995; Kadmon 1995; Worthen & Rhode 1996; Wright et al. 1998). The possibility that nestedness of critical resources also can produce nested species distributions has been raised often (Cody 1983; Simberloff & Martin 1991; Cook & Quinn 1995; Wright et al. 1998; Ricklefs & Lovette 1999), but only rarely tested empirically (Calmé & Desrochers 1999; Honnay et al. 1999). We used data for resident butterflies in the Toquima Range in the Great Basin of the western United States to examine the role habitat features may play in generating nested distributional patterns.

“Ordering” the presence/absence matrix

Presence/absence matrices for nestedness analysis typically are assembled by listing locations as rows in order of decreasing species richness and species as columns in order of decreasing ubiquity. This ordering is phenomenological: it provides a description of assemblage composition (cf. Worthen 1996) but contributes little toward understanding agents that drive assemblage structure. If one wishes to test whether a particular environmental variable may be related to a nested distributional pattern (by correlation if not causation), then rows instead may be ordered with respect to that variable. For example,

listing rows in order of decreasing area quantifies the degree to which faunas are nested by area (Lomolino 1996; Deacon & Mac Nally 1998; Honnay et al. 1999; Mac Nally & Lake 1999). Matrix reordering was used in the analyses presented here, in which we identify influential topographic elements that generate the most strongly nested patterns and are more informative than purely phenomenological ordering by richness.

Study system

The Great Basin includes more than 200 mountain ranges. After the Pleistocene, these ranges were isolated from the surrounding lower-elevation valleys as the regional climate became warmer and drier (Brown 1978; Wells 1983; Grayson 1993). Individual mountain ranges function as discrete habitat islands for many taxa that either are restricted to montane habitats or have relatively low mobility (McDonald & Brown 1992; Murphy & Weiss 1992). For many resident butterflies (taxa that complete their entire life cycle in the mountain range), canyons or segments of canyons within mountain ranges also represent networks of habitat islands (Fleishman et al. 1997; Fleishman & Murphy 1999).

Our study system met three key assumptions of most of the common nestedness analyses (Patterson & Atmar 1986; Patterson 1987; Wright & Reeves 1992; Atmar & Patterson 1993; Wright et al. 1998). First, locations had a common biogeographic history. Second, locations shared an ancestral pool of species. Third, relatively complete species inventories had been conducted.

METHODS

Data for our analyses were collected from 1996–1999 in 10 canyons in the Toquima Range, a ~1750 km² mountain range in the central Great Basin (Lander and Nye counties, Nevada, U.S.A.). We divided canyons into multiple segments from base to crest, each segment extending for approximately 100 m in elevation and 100 m in width (Fleishman et al. 1998, 2001a). More than 75% of the segments were > 1 km long. Although the segments within a canyon were not completely “independent,” spatially or faunally, this is not a confounding factor because nestedness analyses, especially differential-colonization models, assume that there is some dispersal between patches or islands (Worthen 1996). In addition, the short-term presence of species in each locality is independent (i.e., individuals are not shared among localities) (Fleishman et al. 2000). Fewer than 25% of the butterfly species in the Toquima Range disperse more than a few hundred meters (Fleishman et al. 1997). Therefore, recording a species from a given canyon segment implies that the species breeds in that segment. The dynamics of some populations may be linked (Brown & Kodric-Brown 1977; Hanski & Gilpin 1997), but measurement of species occurrence should not be hampered by movement among canyon segments. Moreover, our focus here is on relative nestedness of different matrix-ordering criteria, so absolute nestedness is not critical.

We conducted comprehensive inventories of butterflies in 49 segments, covering an elevational gradient from 1872 to 2750 m and an area gradient from 5.1 to 45.8 ha. Our inventories followed standard methods for butterflies in temperate regions (Shapiro 1975; Thomas & Mallorie 1985; Swengel 1990; Kremen 1992; Pollard & Yates 1993; Harding et al. 1995); these methods are described in detail in Fleishman et al. (1998). It is reasonable to interpret that a given butterfly species is absent if the area has been searched with these methods during the appropriate season and weather conditions (Pullin 1995; Reed 1996). We recorded 56 resident species of butterflies from our study locations. Detailed life-history

information on these species is presented in Fleishman et al. (1997, 1999). The presence/absence matrix is available from EF upon request.

To assess statistically the relative importance of different ordering variables, we computed the relative nestedness (C) of each matrix (i.e., the one data set [56 species by 49 locations] ordered using different criteria) with the program NESTCALC (Wright et al. 1990). To test whether matrices were significantly nested, we used Cochran's Q statistic (Wright & Reeves 1992). We used Z scores (standard-Normal variates) to test whether significant differences existed in relative nestedness among matrices (Wright & Reeves 1992).

We first computed the relative nestedness of matrices in which rows were listed in order of decreasing species richness and decreasing area of the canyon segment. Because our primary interest was to understand factors that may influence species composition, we also ordered the locations-by-species matrix according to several environmental variables that were suggested by Poisson-based modeling (Mac Nally et al. 2003). These variables, described in detail in Fleishman et al. (2001b), explained significant deviance in the species richness of butterflies in the same set of locations we considered here. Our "best" model of species richness included mean elevation of each canyon segment (ELEVX), the standard deviation of topographic exposure within a 150-m radius (EX150S), and an interaction term involving ELEVX and EX150S. Both variables are associated with several factors that can affect butterfly distributions, including richness and abundance of larval hostplants, adult nectar sources, and potential locations for seeking mates. Exposure is calculated by comparing the elevation of the canyon segment with the elevation of a specified neighborhood around that segment. Thus, EX150S is analogous to local topographic heterogeneity. The best model (henceforth, "full model") explained a highly statistically significant percentage of the total deviance in species richness (46%, $p < 0.0001$). Area did not have significant explanatory power. In our study system, area was not significantly correlated with species richness or topographic heterogeneity and, therefore, did not confound analyses focused upon those variables. Lack of a correlation between area and topographic heterogeneity was partly an artefact of our sampling design: large canyon segments tended to be relatively flat. Although area was correlated with elevation, species richness increased with increasing elevation, whereas area decreased with increasing elevation.

Therefore, we used nestedness analyses to examine whether environmental variables not only were associated with species richness but also might be generating nested species distributions. We do not necessarily imply that the environmental variables directly influence nestedness. It is possible that they do so indirectly, perhaps through determining the distribution of larval hostplants, adult nectar sources, or other important resources. We computed the relative nestedness of matrices with rows ordered by the full model, by ELEVX alone, by EX150S alone, and by the model without the interaction term ("partial model"). To help assess whether the key environmental factors we identified were artefacts, we also computed the relative nestedness of matrices ordered by three environmental variables that did not explain significant variance in species richness: (1) mean "northness" on a scale from -100 (south-facing) to 100 (north-facing) (NORX), (2) mean slope in degrees (SLOPEX), and (3) mean solar insolation in kJ at the vernal equinox (EQINX).

RESULTS

The distributional pattern of Toquima Range butterflies was significantly nested regardless of how the matrix rows were ordered ($p < 0.001$, Table 1). Therefore, the butterfly faunas in relatively depauperate sites are statistically proper subsets of the species present in relatively species-rich locations. Values of the relative nestedness index C for matrices ordered with respect to species richness and the full model were higher than the mean C computed for terrestrial invertebrates on habitat islands (0.403) by Boecklen (1997). The values for species richness, full model, partial model, ELEVX, EX150S, and SLOPEX all were within the range of reported values for other lepidopteran communities (Cook & Quinn 1995; Boecklen 1997).

The matrix ordered by species richness was significantly more nested than matrices ordered by environmental variables or combination of variables, including area and the full model (Table 2). This result is not very surprising, nor is it highly informative for understanding variables associated with richness patterns or for land-use planning. The more important and potentially useful result is that the matrix ordered by the full model was significantly more nested than those ordered by area, the partial model, or any other environmental variable (Table 2). These results indicate that in our study system, not only species richness (as revealed by Poisson-based modeling, Mac Nally et al. 2003) but also species composition (as revealed by nestedness analyses) are better modeled as functions of environmental variables (ELEVX, EX150S) that do not include area. The matrix ordered by the full model was significantly more nested than those ordered by NORX, SLOPEX, or EQINX, indicating that the full model is unlikely to be an artefact.

DISCUSSION

Species richness often increases as area increases. Not only population size but also the diversity of ecological “opportunities” tends to be positively correlated with area (MacArthur & Wilson 1967; Ricklefs & Lovette 1999). In a nested system, therefore, species-rich locations commonly are relatively large, whereas depauperate sites are relatively small. The butterflies of the Toquima Range have a significantly nested distributional pattern. Although our study system is nested, it is unusual in that area is not correlated with species richness. The range of areas we sampled was reasonably extensive, so inadequate sampling with respect to area is unlikely to be responsible for the lack of an area effect. Area appears to have had less influence in generating the nested pattern than has the combination of elevation and topographic heterogeneity or resources correlated with elevation and topographic heterogeneity. Instead, our results likely reflect that area was not positively correlated with two environmental factors that do appear to drive species richness. Elevation covaried with both species richness and area, but the former correlation was positive and the latter correlation was negative (Fleishman et al. 2000). Topographic heterogeneity also was not significantly correlated with area (again, probably because large canyon segments tended to be relatively flat).

What are the ecological explanations for why elevation and topographic heterogeneity influence the richness and compositional pattern of butterflies in the Toquima Range? Elevational gradients affect the distributions of numerous taxa, including butterflies, in diverse geographic regions (e.g., Merriam 1890; Terborgh 1977; Baz 1987; Kremen 1994; Yu 1994; Fernández-Palacios & de Nicolás 1995; Lieberman et al. 1996). Elevation probably is correlated with species richness of butterflies in ranges throughout the Great Basin,

although the functional relationship between the two variables seems to differ between mountain ranges (Fleishman et al. 1998, 2000). In the nearby Toiyabe Range, for example, there is a negative correlation between elevation and species richness of butterflies (Fleishman et al. 1998). In the Toquima Range, the positive correlation between species richness and elevation seems to reflect a gradient in climatic severity (Fleishman et al. 2000). Low elevations in the Toquima Range are arid and floristically depauperate. As a result, larval hostplants, adult nectar sources, and some potential locations for seeking mates are scarce; this scarcity can increase butterfly mortality. Conditions at upper elevations in the Toquima Range are moderately harsh (e.g., relatively cool and windy), but because much of the Toquima crest is not high-elevation in an absolute sense (~2700 m), climate may constrain species richness less at high elevations than at low elevations.

Species richness of butterflies in the Toquima Range also increases with increasing topographic heterogeneity as represented by EX150S. Varied topography likely supports a correspondingly diverse plant community in terms of both composition and structure. Topographic heterogeneity also affords numerous locations for seeking mates (Scott 1975, 1986) and may provide shelter from extreme weather events.

Given the variance in functional relationships between species richness of butterflies and some environmental variables among mountain ranges, it is fair to ask how general the results of this study are likely to be and what analyses of nestedness realistically contribute to land management. Our ongoing work throughout the Great Basin increasingly suggests that although the *shape* of the relationship between species richness and those independent variables may not be uniform, the *significance* of that relationship is much more consistent. The nestedness analyses we present are valuable because they indicate that certain variables influence species composition and the distribution of species richness. For instance, a manager who had performed the same analyses we present here might recommend to a colleague with responsibility for a different (unanalyzed) mountain range that he or she factor elevation and topography as well as area into the decision-making process. In many cases, a relatively rapid and tractable field inventory might be adequate to verify the shape of the relationship between species richness and elevation (for example) in the second range.

More generally, the fact that nestedness metrics integrate information on both richness and composition renders them a useful complement to analyses that focus on just one of these components (Margules & Pressey 2000). Species richness is a major variable for conservation and land-use planning, especially when financial and human resources are limited. Yet species composition, particularly the distribution of relatively rare versus relatively ubiquitous taxa, also plays a crucial role in allocating locations for a suite of potential land uses. Consideration of both richness and composition—by any method—is more important for conservation purposes than the method itself. In other words, we do not propose nestedness analyses as a panacea for all situations. Nestedness metrics are only one of many analytic tools available to ecologists and practitioners. But nestedness analyses do offer several practical advantages which may be important in some contexts. For example, nestedness is relatively intuitive and is easier to calculate than many alternative distribution models, which are more computationally intensive and may require substantial technical resources and specialized knowledge (Guisan & Zimmerman 2000). These considerations are particularly important when funding is limited and there is an immediate need for management guidance.

A key implication and advantage of our results is that among at least some taxonomic groups, faunal richness and compositional patterns are related to independent variables that can be measured extensively—through remote sensing and subsequent processing—reducing dependence on intensive measurements of habitat. This is important because in rugged landscapes like the Great Basin, more than 75% of which is managed by federal agencies, we often lack even baseline knowledge about species distributions. Without this information, it is difficult to address the viability of many native species. If an assemblage is nested, and analyses indicate that environmental correlates with that pattern can be derived for locations where species inventories have not yet been conducted, then it should be possible to predict the relative, if not the absolute, contribution various locations may make to regional species richness of that taxonomic group and to the species composition of those locations. These estimates help in ranking locations for an array of activities including protection, resource extraction, recreation, restoration, and more detailed field studies.

Further, our results emphasize that factors like topographic diversity probably should be considered explicitly when extensive land-use plans are being developed. This recommendation initially may seem trivial: to most biologists, evidence of a relationship between species richness and putative habitat diversity, for example, is not particularly surprising. In our experience, however, fads can create pressure on managers to overlook basic ecological relationships during the biodiversity planning process. During the late 1990s, for instance, managers in the western United States frequently were urged to maximize the percentage of the landscape in a high “seral stage” despite the fact that a mosaic of vegetation associations and successional stages often is associated with greater faunal diversity. Efforts to increase representation of high seral vegetation often were based on the general misunderstanding that seral stage is correlated with human land use and only with human land use. The latter misconception did not account for potential correlations between seral stage and natural disturbance processes. Nor did it recognize that correlations between species richness and either seral stage or human land use often are not linear.

Although we believe our work has implications for many ecosystems and taxonomic groups, our results also could be used to develop specific guidelines for prioritizing locations for various land uses. We emphasize that these specific guidelines are used for illustrative purposes: different guidelines likely would apply to other landscapes and assemblages. For example, we would not suggest that extractive uses be barred from all high elevation and topographically heterogeneous areas. We would, however, advocate restricting high-impact human land uses in at least some high elevation and topographically heterogeneous areas. Conservation biologists and practitioners often assume that all else being equal, species richness is correlated with area. In our study system, elevation and topography are potential sources of discrimination. In other words, if one of two equal-area locations must be designated as wilderness and one as an active grazing allotment, the more heterogeneous site probably should be protected.

There can be some variation among canyons within a mountain range in the relationship between species richness of butterflies and environmental variables. However, ecologically significant range-level “signals” with respect to species distribution patterns generally can be detected despite some background canyon-level “noise.” Thus, while one should not assume that species richness and elevation are positively correlated in each and every canyon, the overall pattern reasonably can be expected to hold for canyons in which species inventories have not yet been conducted (Fleishman and Mac Nally, unpublished data).

The combination of a robust model and rational thought can be quite powerful, but no model is a substitute for common sense. If we protect several locations within a mountain range that have relatively high species richness of butterflies, our results suggest we can assume that local assemblages elsewhere in the range are subsets of the protected assemblages. However, some species of concern (e.g., rare or highly sensitive to human disturbance) inevitably will not be present in the most species-rich locations. Virtually every nested assemblage has a few unexpected presences (“outliers”) and absences (“holes”). Nestedness analyses should be viewed not as a universal solution but as a potential shortcut for land use planning when data, time, and money are constrained.

It is not our intention to imply absence of a relationship between species richness—of butterflies or of any other taxon—and area. We concentrated on patterns within a mountain range; relatively large mountain ranges well may have more species than smaller mountain ranges (Boggs & Murphy 1997; but see Lawlor [1998], who found that the correlation between species richness of mammals and mountain range area was weaker than previously thought). At minimum, however, it is clear that significant correlations between species richness and area are not consistent across spatial scales, and that area may not necessarily be the best predictor of species richness.

Our results, and those of related studies, should prove useful even if they prove applicable only to a single taxonomic group. Managers frequently are responsible for minimizing species losses among all plants and animals. Furthermore, some taxonomic groups (butterflies among them) are relatively easy to study and monitor and have served as popular “flagships” for education and public engagement (Simberloff 1998; Caro & O’Doherty 1999). Thus, we believe nestedness analyses are promising tools not only for describing patterns of community composition, but also for conservation planning in the broad sense. We advocate analyses of other data sets by ordering presence/absence matrices according to topographic or habitat variables in addition to area and species richness. Such analyses may reveal, or at least suggest for further analysis, more fundamental causes of nestedness than do the basic descriptions of pattern.

GLOSSARY

Differential colonization. The order in which species initially colonize an area is thought to be influenced by their vagility and opportunism. All else being equal, species with large movement distances and relatively general resource requirements are expected to be among the first to colonize an area.

Idiosyncratic species. A species with a distribution that appears to be affected by biogeographic factors different from those affecting the assemblage as a whole.

Nested. A nested biota is one in which the species present in depauperate locations are subsets of the species present in locations that are richer in species.

Nonrandom extinction. Biological communities are composed of species whose inherent susceptibilities to extinction differ as functions of population size, trophic status, habitat specialization, and myriad other life history characteristics. Although environmental stochasticity often exacerbates or alleviates these largely deterministic risks, patterns of nonrandom local species disappearances may be nonrandom.

Poisson distribution. A probability distribution for discrete variables that usually describes variables representing the number of occurrences (which often may be rare) of a particular event in an interval of time or space, such as counts.

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Table 1. Values of the relative nestedness index C for matrices with different row-ordering criteria. Each matrix included the same 49 locations and 56 species. The full model included mean elevation of each canyon segment (ELEVX), the standard deviation of topographic exposure within a 150-m radius (EX150S), and an interaction term involving ELEVX and EX150S. The partial model included ELEVX and EX150S, but not the interaction term. NORX refers to mean “northness” on a scale from -100 (south-facing) to 100 (north-facing), SLOPEX refers to mean slope in degrees, and EQUINX refers to mean solar insolation in kJ at the vernal equinox.

| Row order | C^1 |
|------------------|-------|
| Species richness | 0.494 |
| Full model | 0.457 |
| Partial model | 0.375 |
| Area | 0.278 |
| ELEVX | 0.364 |
| EX150S | 0.354 |
| NORX | 0.275 |
| SLOPEX | 0.353 |
| EQINX | 0.268 |

¹ Degrees of freedom (55), Q (885.64), and p values (< 0.001) were identical for all analyses.

Table 2. Pairwise comparison among values of the relative nestedness index C for matrices with different row-ordering criteria. S = species richness. The full model included mean elevation of each canyon segment (ELEVX), the standard deviation of topographic exposure within a 150-m radius (EX150S), and an interaction term involving ELEVX and EX150S. The partial model included ELEVX and EX150S, but not the interaction term. NORX refers to mean “northness” on a scale from -100 (south-facing) to 100 (north-facing), SLOPEX refers to mean slope in degrees, and EQUINX refers to mean solar insolation in kJ at the vernal equinox.

| Orderings compared | Z | p^2 |
|------------------------------|---------|----------|
| S vs. full model | 2.38* | < 0.01 |
| S vs. area | 12.79** | < 0.0001 |
| Full model vs. area | 11.38** | < 0.0001 |
| Full model vs. partial model | 5.24** | < 0.0001 |
| Full model vs. ELEVX | 5.91** | < 0.0001 |
| Full model vs. EX150S | 6.55** | < 0.0001 |
| Full model vs. NORX | 11.58** | < 0.0001 |
| Full model vs. SLOPEX | 6.64** | < 0.0001 |
| Full model vs. EQUINX | 12.08** | < 0.0001 |

² p values are one-tailed (Wright & Reeves 1992).